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Published in:
Journal of Animal Ecology

DOI:
10.1111/j.1365-2656.2004.00903.x

Publication date:
2005

Journal of Animal Ecology 2005
74, 105–119

Digestive bottleneck affects foraging decisions in red knots *Calidris canutus*. I. Prey choice

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Summary

1. Rate-maximizing foragers that only divide their time between searching and handling prey should, according to the classical contingency model (CM), only select those prey whose energy content per unit handling time (i.e. profitability) exceeds or equals long-term average energy intake rate.
2. However, if digestively constrained foragers were to follow this so-called 'zero-one rule', they would need to take digestive breaks and their energy intake over total time would not be maximized. They should, according to the digestive rate model (DRM), also consider the rate at which a prey type is digested (i.e. digestive quality), such that time lost to digestive breaks is minimized.
3. In three different contexts, we tested these competing models in a mollusc-eating shorebird, the red knot (*Calidris canutus*), that is often digestively constrained due to its habit of ingesting its bulky prey whole. Measurements on gizzard size (using ultrasonography) and prey-characteristics confirmed that in each test the birds were digestively bottlenecked and should thus follow the DRM in order to maximize long-term energy intake.
4. In the first experiment, knots were offered a choice between two fully exposed prey, and tended to select prey by the criterion of digestive quality rather than profitability.
5. In the second experiment, knots were offered two buried prey types and preferred the highest quality prey to the most profitable prey.
6. In the wild, knots mainly fed on high quality *Mya* and largely ignored poor quality, but equally profitable, *Cerastoderma*.
7. Thus, each test verified the predictions of the DRM and rejected those of the CM. Given that many species face digestion constraints, we expect that the DRM is likely to explain diet composition in many more studies.

Key-words: contingency model, digestive constraint, digestive rate model, foraging decision, gizzard, intake rate, optimal diet, optimal foraging theory, patch, prey choice.

Journal of Animal Ecology (2005) **74**, 105–119
doi: 10.1111/j.1365-2656.2004.00903.x

Introduction

Prey selection has profound effects on stability of predator-prey dynamics (Fryxell & Lundberg 1994) and coexistence between competing prey (Paine 1966; Holt & Kotler 1987). The mechanisms underlying food preferences are therefore essential components of community ecology. Ever since the publication of a seminal paper by MacArthur & Pianka (1966), the mainstream prey-selection studies have approached the problem from an optimality perspective, of which the so-called contingency model (CM) is best known (Pulliam 1974; Charnov 1976; also called the prey model by Stephens & Krebs 1986). For a predator that aims to maximize its long-term average energy intake rate, the CM predicts which prey types should be accepted. A prey type i is characterized by its metabolizable energy content e_i and required handling time h_i. The optimal decision rule, the so-called 'zero-one' rule, is simple: prey types whose profitability (e_i/h_i) exceeds or equals long-term average energy

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intake rate should be included in the diet, while those prey types with lower profitabilities should be ignored.

The CM has been developed for so-called 'handling-limited' foragers (Farnsworth & Illius 1998), i.e. animals that spend all of their time foraging (handling and searching) and whose maximum rates of energy intake are ultimately constrained by the rate at which prey can be externally handled (Jeschke, Kopp & Tollrian 2002). However, as recently concluded by Jeschke *et al*. (2002), rates of energy intake are mostly constrained by digestion rates rather than by handling rates. Whenever rate of digestion constrains rate of energy intake (i.e. a digestive bottleneck; Kenward & Sibly 1977), a forager may need to take digestive pauses before any new prey item can be ingested (e.g. Van Gils *et al*. 2003b). A forager obeying 'contingency-rules' would maximize its energy intake per unit foraging time (i.e. short-term intake rate, cf. Fortin, Fryxell & Pilote 2002) but not necessarily per unit total time (i.e. foraging plus digestive pauses; long-term intake rate, cf. Fortin *et al*. 2002). In fact, whenever prey types differ in the rate at which they can be assimilated (W), a digestively constrained forager obeying the CM does not maximize its energy intake over total time (Verlinden & Wiley 1989). If natural selection acts primarily upon energy intake over total time (Stephens & Krebs 1986), a digestively constrained forager should be selective towards prey types that can be digested rapidly. Time which otherwise would be lost to digestive pauses can then be used to search for easy-to-digest prey types (Verlinden & Wiley 1989; Hirakawa 1997a).

The so-called digestive rate model (DRM) predicts optimal diets that maximize long-term energy intake rate in such digestion-constrained situations (Verlinden & Wiley 1989 as amplified by Hirakawa 1997a; Hirakawa 1997b; Farnsworth & Illius 1998; as adjusted by Fortin 2001). DRM is structurally similar to the CM in the sense that prey types can be ranked in terms of rate of energy uptake. In fact, the CM's 'zero-one' rule emerges from the DRM as an optimal solution for the (restricted) case that rate of energy intake is 'handling-limited'. The best-known alternative diet model that considers a digestive constraint, the linear programming model (LPM; Belovsky 1978, 1984, 1986), has been criticised for its inability to consider many prey types and for being circular (Owen-Smith 2002). DRM lacks these limitations.

It is interesting to note that although digestive constraints are believed to be widespread (Masman *et al*. 1986; Prop & Vulink 1992; Kersten & Visser 1996; Guillemette 1998; De Leeuw 1999; Jeschke *et al*. 2002; Karasov & McWilliams 2004), and food preferences are often explained in the light of digestive bottlenecks (Kenward & Sibly 1977; Bustnes & Erikstad 1990; Zwarts & Blomert 1990; Kaiser *et al*. 1992), actual explicit tests of optimal diet models that consider a digestive bottleneck have mainly been restricted to herbivores (Westoby 1974; Belovsky 1978; Owen-Smith & Novellie 1982; Vivås, Sæther & Andersen 1991; Shipley *et al*. 1999; see Hoogerhoud 1987 for an application to molluscivorous cichlids). In most of these cases, LPM or modified versions of the CM were tested; tests of DRM have been rare up to now (but see Fortin *et al*. 2002; Illius *et al*. 2002).

In this study we provide, to the best of our knowledge, the first explicit test of a DRM in a nonherbivore. Our study species is the red knot (*Calidris canutus*), a medium-sized shorebird that lives in intertidal habitats where it feeds mostly on molluscs. Due to their habit of swallowing prey whole, a lot of bulky, indigestible ballast (shell) material enters the digestive tract (80–90% of total prey dry mass; Zwarts & Blomert 1992). As their buried prey are detected relatively efficiently by a pressure-sensory system in the bill tip (Piersma *et al*. 1998) and as handling times are relatively short (Zwarts & Wanink 1993; Piersma *et al*. 1995), digestive processing rates often cannot keep up with rates of prey encounter and ingestion. Thus, energy intake of red knots tends to be digestion- rather than handling-limited (Van Gils *et al*. 2003a, 2003b, 2005; Van Gils & Piersma 2004). It turns out that the constraining link in the chain of digestive processes is the rate at which shell mass is crushed and processed, and that knots can alleviate this constraint to a certain extent by flexibly increasing the size of the crushing organ, the muscular gizzard (Dekinga *et al*. 2001; Van Gils *et al*. 2003a). The relative ease with which we can (1) measure available prey densities (Zwarts, Blomert & Wanink 1992; Piersma *et al*. 1993b; Piersma, de Goeij & Tulp 1993a; Piersma, Verkuil & Tulp 1994) (2) experimentally manipulate prey densities (Piersma *et al*. 1995; Van Gils *et al*. 2003b) (3) reconstruct diet composition (Dekinga & Piersma 1993) (4) experimentally quantify handling and searching times (Piersma *et al*. 1995), and (5) noninvasively estimate gizzard mass as a predictor of digestive processing capacity (see below; Dietz *et al*. 1999), makes the knot an ideal species to study factors determining prey choice. Our objective here is to test, both under controlled laboratory conditions and in the wild, whether prey choice by red knots follows the predictions of the CM or those of the DRM.

THE DIGESTIVE RATE MODEL

The DRM applied here (Hirakawa 1995) assumes that knots aim to maximize long-term average metabolizable energy intake rate Y, under the constraint that ballast mass intake rate X does not exceed a specific threshold. Metabolizable energy intake rate Y (W) while foraging is given by (notation follows Stephens & Krebs 1986 and Hirakawa 1995):

$$Y = \frac{\sum \lambda_i p_i e_i}{1 + \sum \lambda_i p_i h_i} \qquad \text{(eqn 1)}$$

where λ_i is encounter rate (s^{-1}) with items of prey type i (= 1, … , n), p_i is the probability that type i is accepted upon encounter, e_i is the metabolizable energy content (J) of type i, and h_i is the time (s) required to handle type

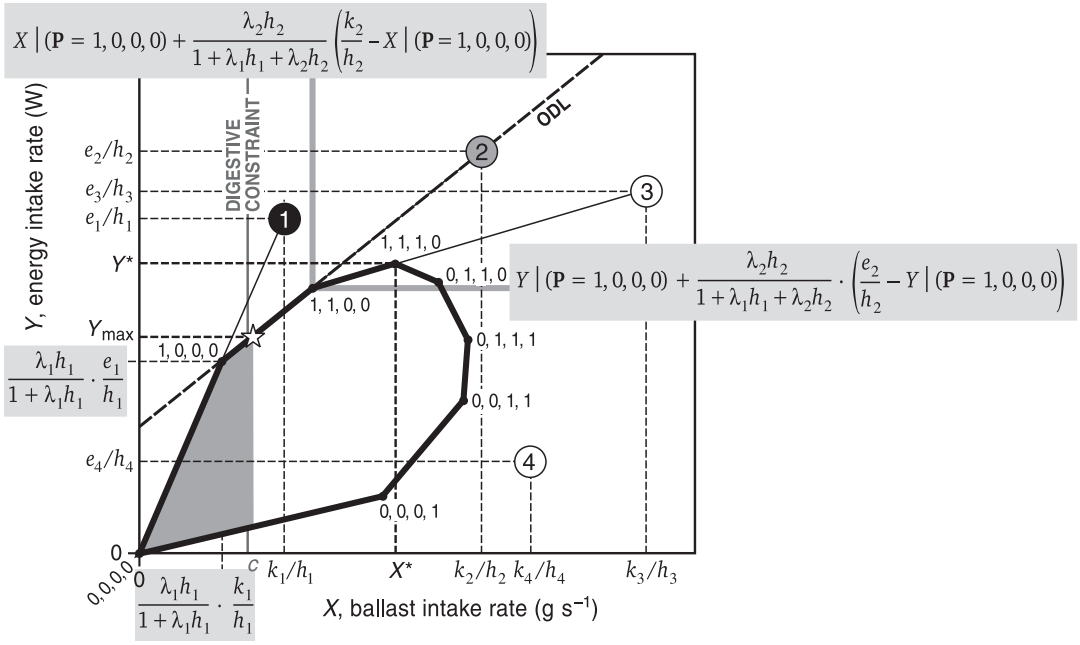

Fig. 1. The optimal diet when digestively constrained can be found by the graphical procedure of the digestive rate model (DRM). In this example, numbered dots denote profitability e_i/h_i (W) vs. ballast mass/handling time k_i/h_i (g s^{-1}) for each prey type $i = 1, \ldots, 4$. Thick-lined loop represents boundaries on feasible short-term intake rates (i.e. while foraging) in terms of ballast mass (X; horizontal axis) and energy (Y; vertical axis). Which short-term intake rate (X, Y) is obtained within this so-called 'feasible region' depends on the predator's prey choice $\mathbf{P} = (p_1, p_2, p_3, p_4)$, whose values are indicated at each corner of the feasible region. Of course, ignoring all prey types ($\mathbf{P} = 0, 0, 0, 0$) yields no intake (X, $Y = 0, 0$); including only the first prey type (defined as the type of highest digestive quality e_i/k_i; $\mathbf{P} = 1, 0, 0, 0$) yields X, $Y = [\lambda_1 h_1/(1 + \lambda_1 h_1)] \cdot (k_1/h_1), [\lambda_1 h_1/(1 + \lambda_1 h_1)] \cdot (e_1/h_1)$. Adding the second best quality type to this ($\mathbf{P} = 1, 1, 0, 0$) adds $\lambda_2 h_2/(1 + \lambda_1 h_1 + \lambda_2 h_2) \cdot [(k_2/h_2) - X \mid (\mathbf{P} = 1, 0, 0, 0)]$ and $\lambda_2 h_2/(1 + \lambda_1 h_1 + \lambda_2 h_2) \cdot [(e_2/h_2) - Y \mid (\mathbf{P} = 1, 0, 0, 0)]$ to, respectively, X and Y, etc. (see Hirakawa 1995 for more details). Including the third best quality type yields maximal energy intake rate while foraging (defined as Y^*). However, in this example rate of ballast intake X^* associated with Y^* cannot be sustained in the long run due to limited capacity c of the digestive system (indicated by grey vertical line); the predator faces a so-called digestive constraint. Grey area left of c indicates what intake rates (X, Y) can be sustained in the long run. In order to maximize long-term energy intake (indicated by star at Y_{max}), the predator should therefore only accept prey type 1 (solid dot) and a proportion of prey type 2 (grey dot; $\mathbf{P} = (1, 0{\cdot}3, 0, 0)$). This diet composition can easily be deduced from the so-called optimal diet line (ODL indicated by diagonal dashed line), which is the line tangent to the feasible region at (c, Y_{max}) and separates types that are included in the diet (above the ODL) from those that are excluded (below the ODL). The one type that is at the ODL (in this case type 2) should be partially preferred. Note that according to the CM, types whose $e_i/h_i = Y^*$ should be accepted, i.e. $\mathbf{P} = (1, 1, 1, 0)$.

i. Recall that this is the familiar Holling's disc equation in a multiple prey context (Holling 1959; Charnov 1976). Similarly, ballast material intake rate X (g s^{-1}) while foraging is given by:

$$X = \frac{\sum \lambda_i p_i k_i}{1 + \sum \lambda_i p_i h_i} \qquad \text{(eqn 2)}$$

where k_i is the ballast mass of prey type i. The digestive constraint is expressed as

$$X \leq c \qquad \text{(eqn 3)}$$

where c is maximum digestive capacity (g s^{-1}), expressed as the upper limit on long-term ballast intake rate X.

Hirakawa (1995) presented a (graphical) solution procedure of the problem to find $\mathbf{P} = (p_1, p_2, \ldots, p_n)$ that maximizes Y under constraint $X \leq c$. First, for each prey type i, profitability (i.e. the ratio e_i/h_i) is plotted vs. the ratio ballast mass/handling time (k_i/h_i). Second, in the same graph, the so-called 'feasible region' is plotted, that is the region that contains the X-Y data for all possible prey choice strategies, that is for all possible vectors $\mathbf{P}$. The term 'feasible' refers to what intake rates are feasible while foraging (short-term) within the constraints of food environment $\mathbf{F} = (\mathbf{f_i}) = ([e_i, k_i, h_i, \lambda_i])$. Hirakawa (1995) provides a very elegant graphical procedure to find the boundaries of the feasible region in a relatively simple and straightforward manner. Basically, the procedure starts with including the prey type with the highest ratio e_i/k_i (which will be called 'quality' or 'digestive quality' cf. Verlinden & Wiley 1989) as the first prey type in the diet. This gives:

$$X \mid (\mathbf{P} = 1, 0, \ldots, 0) = \frac{\lambda_1 k_1}{1 + \lambda_1 h_1} = \frac{\lambda_1 h_1}{1 + \lambda_1 h_1} \cdot \frac{k_1}{h_1} \qquad \text{(eqn 4)}$$

and

$$Y \mid (\mathbf{P} = 1, 0, \ldots, 0) = \frac{\lambda_1 e_1}{1 + \lambda_1 h_1} = \frac{\lambda_1 h_1}{1 + \lambda_1 h_1} \cdot \frac{e_1}{h_1} \qquad \text{(eqn 5)}$$

Hence, graphically, the bivariate point X, $Y \mid (\mathbf{P} = 1, 0, \ldots, 0)$ is located on the line that connects the origin (0, 0) with the point (k_1/h_1, e_1/h_1). See Fig. 1. Including a second prey type in the diet gives:

$$X\,|\,(\mathbf{P} = 1, 1, 0, \ldots, 0) = \frac{\lambda_1 k_1 + \lambda_2 k_2}{1 + \lambda_1 h_1 + \lambda_2 k_2}$$

$$= \frac{\lambda_1 h_1}{1 + \lambda_1 h_1} \cdot \frac{k_1}{h_1} + \frac{\lambda_2 h_2}{1 + \lambda_1 h_1 + \lambda_2 h_2}\left(\frac{k_2}{h_2} - \frac{\lambda_1 h_1}{1 + \lambda_1 h_1} \cdot \frac{k_1}{h_1}\right) \quad \text{(eqn 6)}$$

and thus

$$X\,|\,(\mathbf{P} = 1, 1, 0, \ldots, 0) = X\,|\,(\mathbf{P} = 1, 0, \ldots, 0) + \frac{\lambda_2 h_2}{1 + \lambda_1 h_1 + \lambda_2 h_2}\left(\frac{k_2}{h_2} - X\,|\,(\mathbf{P} = 1, 0, \ldots, 0)\right) \quad \text{(eqn 7)}$$

and similarly for $Y\,|\,(\mathbf{P} = 1, 1, 0, \ldots, 0)$. Hence, point $X, Y\,|\,(\mathbf{P} = 1, 1, 0, \ldots, 0)$ is located on the line that connects point $X, Y\,|\,(\mathbf{P} = 1, 0, \ldots, 0)$ with point $(k_2/h_2, e_2/h_2)$, and so forth (Fig. 1). By a clever choice of new points to be included in the diet (or excluded again), one can graph the boundary lines of the feasible region quite easily. For details we refer to the original paper (Hirakawa 1995). It can further be shown that the boundary line at the optimal X, Y point (recall that the optimal point has maximum Y, defined as Y_{max}, while still obeying $X \leq c$ in the long run) separates those prey types that are included in the diet from those that are excluded (the so-called 'Optimal Diet Line' ODL; Fig. 1).

TESTING THE DRM AGAINST THE CM

We provide three tests of the DRM against the CM. The first is an experimental test of preference for 11 different prey types (different size classes of 5 different prey species) that were offered pairwise, unburied, and *ad libitum* to single (captive) knots (Fig. 2A–B). Given the birds' gizzard masses and high short-term intake rates (since no search time was required), these experimental conditions ensured long-term energy intake rate to be digestion- rather than handling-limited. Under these conditions, the CM, which ignores digestive constraints, predicts that only the most profitable (e/h) prey should be preferred (Fig. 2A). In contrast, the DRM predicts that only prey of the highest digestive quality (e/k) should be taken (Fig. 2B).

The second test is an experiment where two buried prey types (two size classes of a single species) were offered pairwise in low densities to single (captive) red knots. The most profitable prey type was lowest in digestive quality and occurred in higher densities than the less profitable but higher quality prey (Fig. 2C–D). Given experimental conditions (gizzard masses and short-term intake rates), the CM predicts the higher quality prey type should be completely ignored ($P = 0$), while the lower quality prey type should be completely accepted ($P = 1$; Fig. 2C). In contrast, the DRM predicts almost the opposite: the higher-quality prey type should be completely accepted ($P = 1$), while the lower quality prey type should only be partially accepted ($0 < P < 1$; Fig. 2D).

The third test is performed on free-ranging red knots in the wild that fed in a natural patch containing multiple prey types of two species. The CM predicts both species to be eaten in equal amounts, while the DRM predicts the diet to be composed mainly of the higher quality prey species.

Materials and methods

EXPERIMENT 1: *AD LIBITUM* EXPOSED PREY IN A SINGLE PATCH

The birds and their holding conditions. Six captive red knots participated in this experiment which was carried out between 11 August and 18 September 2000. All six birds were adult and were caught with mist-nets in the Dutch Wadden Sea in 1994, 1995 and 1999. Ever since their capture these birds had been housed in large in- and outdoor aviaries at the Royal Netherlands Institute for Sea Research (NIOZ, Texel, the Netherlands). The experiment took place outdoors on the island of Griend in the western Dutch Wadden Sea (53°15′-N, 5°15′-E), which facilitated the daily collection of fresh prey specimens. There the birds lived in small holding pens (2·5 × 1 × 0·5 m) and were given *ad libitum* access to water and access to staple food between 6 p.m. and 8 a.m. Staple food comprised edible cockles (*Cerastoderma edule*) and trout pellets (Trouvit, Produits Trouw, Vervins, France).

Every morning each bird was weighed in order to monitor its health and nutritional status. This also allowed us to adjust the daily amount of staple food such that body mass would be kept low (100–120 g). Together with the removal of the staple food at least six hours before the start of a trial (i.e. length of high tide period), this ensured eagerly feeding birds during the trials.

The prey. We offered two prey types pairwise in full view at the same time to an experimental bird; in total we tested preference for 11 different prey types. These were 3 size classes of a bivalve, the Baltic tellin (*Macoma balthica*), 3 size classes of another bivalve, the edible cockle (*Cerastoderma edule*), 1 size class of a gastropod, the mudsnail (*Hydrobia ulvae*), 2 size classes of a crustacean, the shore crab (*Carcinus maenas*), and 2 size classes of another crustacean, the common shrimp (*Crangon crangon*). Size classes were measured using callipers, and were based on mm-classes of length or width (*Carcinus*), and were defined as 5–7 (small), 9–11 (medium), and 13–15 (large) for the two bivalve species, 1–6 for *Hydrobia*, 4–6 (small) and 10–12 (large) for *Carcinus*, and 17–30 (small) and 40–57 (large) for *Crangon*. In the week preceding the experiment all of these prey types were offered to the birds in order to get them acquainted with handling and digesting them.

Experimental protocol. Trials took place in the permanent holding pens by separating the focal-bird from the rest of the flock in part of the pen. In a trial two prey types (10 individuals each) were offered alive and

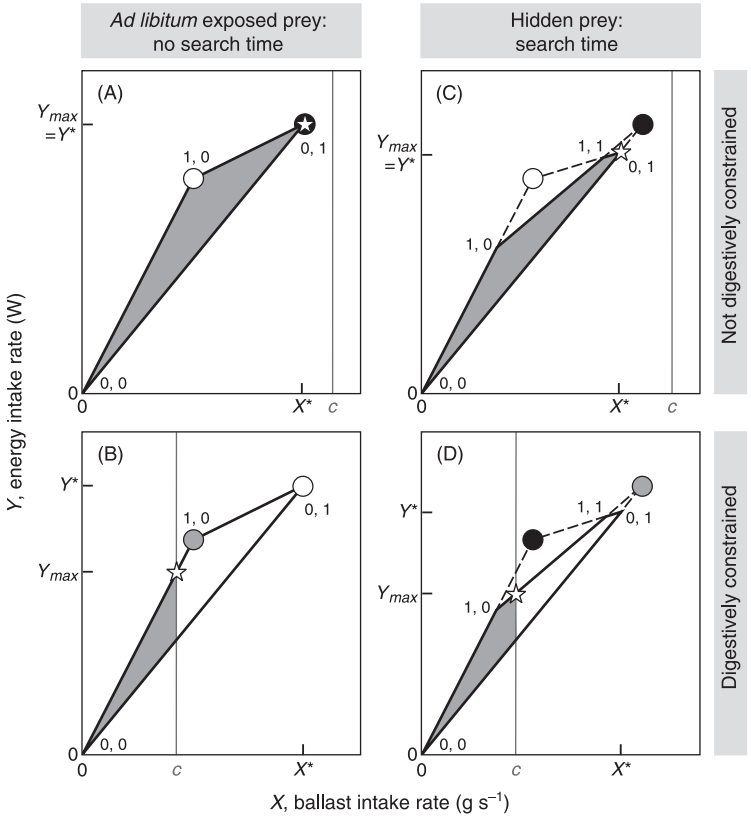

Fig. 2. Solving for the optimal diet by the DRM in a two-prey-type situation. Dots denote e_i/h_i (W) vs. k_i/h_i (g s^{-1}) for each type i. Solid lines indicate borders of the so-called 'feasible region' in which short-term intake rates can vary; at each corner of the region prey choice $\mathbf{P} = (p_1, p_2)$ is indicated (with type 1 being the one with the highest e/k-ratio). Vertical line indicates upper limit on sustainable long-term ballast intake rate X set by digestive constraint c. Grey area indicates set of long-term intake rates that remains when taking short-term feasible region into account. Star indicates long-term intake rate (X, Y) that is achieved when the optimal diet is selected (yielding Y_{max}). In (A) and (B), the two prey types are exposed *ad libitum*. The forager thus requires no search time to find them, i.e. its short-term intake rate is not constrained by encounter rate λ. Therefore short-term intake rates (X, Y) can be as high as k_2/h_2 (= X^*) and e_2/h_2 (= Y^*). In (A), these intake rates can be sustained in the long run (since $c > X^*$), and the forager should therefore include only the most profitable (e/h) prey type in its diet (filled dot), while the other should be entirely ignored (open dot; $\mathbf{P} = (0, 1)$; yielding $Y_{max} = Y^*$). In (B), maximum short-term intake rates can not be sustained in the long run (since $c < X^*$), and the forager should therefore include only a proportion of the encountered highest quality (e/k) prey (grey dot; $\mathbf{P} = (0{\cdot}9, 0)$; alternatively, it could take digestive breaks for 10% of its time while $\mathbf{P} = (1, 0)$). In (C) and (D), the two prey types are hidden and search time is required. Short-term intake rates (X, Y) can thus not be as high as k_2/h_2 and e_2/h_2. In (C), maximum short-term energy intake rate can be sustained in the long run (since $c > X^*$), and the forager should therefore include only the most profitable (e/h) prey type in its diet (filled dot), while the other should be entirely ignored (open dot; $\mathbf{P} = (0, 1)$; yielding $Y_{max} = Y^*$). In (D), this high intake rate cannot be sustained in the long run (since $c < X^*$), and the forager should therefore accept all high-quality prey that it encounters (filled dot), while it should accept only a proportion of the low-quality prey (grey dot; $\mathbf{P} = (1, 0{\cdot}1)$).

unburied on a small platter (0·2 × 0·15 m) to a single bird. Such high densities (667 m^{-2}) of unburied prey ensure that short-term intake rate is not constrained by search time. We aimed to end a trial after five prey ingestions, although occasionally a bird would be less eager to eat and the trial would end after fewer prey had been taken (we were uncertain about what caused such motivational dips; at least they were not related to the combination of prey types on offer). An observer seated 0·5-m from the pen, recorded number of items eaten per type. Our captive knots became tame and did not seem to be bothered by such close distances to humans (see Piersma 2002). As we worked with 11 prey types that were offered pairwise to each bird individually, we performed 55 trials per bird $\left(\binom{11}{2}\right)$; each combination was offered once to each individual, or 330 trials in total (6 × 55). We analysed the 313 trials in which at least one prey choice was made (of which in 292 trials the aimed 5 prey choices were made).

Analysing choice. For each individual bird m separately, we estimated for each prey type i, a cardinal preference rank α_{im}, using the formulation given by Van der Meer (1992):

$$\pi_{ijm} = \frac{e^{\alpha_{im} - \alpha_{jm}}}{1 + e^{\alpha_{im} - \alpha_{jm}}} \qquad \text{(eqn 8)}$$

where π_{ijm} is the probability that prey type i is preferred over prey type j. For this purpose we used the NONLIN-procedure in SYSTAT 10 (Systat Software Inc.).

We subsequently analysed the partitioning of the variance in α_{im} using the GLM-procedure in SYSTAT 10. Cardinal preference ranks possess the convenient property that they can be scaled to characteristics of the prey (e.g. profitability e_i/h_i, or digestive quality e_i/k_i), and that differences on such scale define how partial prey preference will be when two prey types (i and j) are offered simultaneously (Van der Meer 1992, e.g. when $\alpha_{im} - \alpha_{jm} = 0$ then $\pi_{ijm} = 0{\cdot}50$, when $\alpha_{im} - \alpha_{jm} = 1$ then $\pi_{ijm} = 0{\cdot}73$, etc.).

Model parameters. In order to predict prey choice by the CM and the DRM, we modelled how long-term intake rate (X, Y) is constrained by the combination of digestive capacity c and experimental food environment **F**. Besides each bird's digestive capacity c, we therefore measured each prey type's metabolizable energy content e, indigestible ballast mass k, and handling time h.

Digestive capacity. For each bird we determined digestive processing capacity c by ultrasonographically estimating gizzard size (Pie 200 ultrasound, Pie Medical Benelux BV, Maastricht, the Netherlands; see Dietz *et al*. 1999 for details). Duplo-measurements were taken both at the beginning (16 August) and at the end (20 September) of the experiment. We calculated c from gizzard size using Van Gils *et al*. (2003a), who found that the rate at which indigestible ballast material is processed increases quadratically with gizzard mass. This emphasizes the need to ascertain gizzard mass with some precision.

Energy content & ballast mass. By subsampling each prey type we determined dry ballast mass (k) and ash-free dry flesh mass ($AFDM_{flesh}$). In case of the two bivalve species, the soft, fleshy parts were removed from the shell and both shell and flesh were dried to constant mass for three days in a ventilated oven at 55–60 °C. Dry mass of both shell (k) and flesh were determined to the nearest 0·1 g. Subsequently, the dried flesh was incinerated at 550 °C for 2 h, after which the remaining ash mass was subtracted from dry mass to come to $AFDM_{flesh}$. As soft parts could not be separated from hard parts in case of *Hydrobia* and the two crustacean species, we determined dry mass and ash-free dry mass of entire specimens and assumed that 12·5% of organic matter resides in the hard parts of *Hydrobia* (Dekker 1979), and 30% in those of the crustaceans (Zwarts & Blomert 1990). Metabolizable energy content (e) was calculated as $AFDM_{flesh} \times$ energetic density $\times$ assimilation efficiency; the latter two were assumed to be constant across prey types at, respectively, 22 kJ g^{-1} $AFDM_{flesh}$ (Zwarts & Wanink 1993) and 0·725 (Piersma 1994).

Handling time. Handling times were determined in separate trials with the same birds, which were now offered ± 50 items of the same type (i.e. no-choice-trials). Each prey type was offered once to each bird, leading to a total of 66 trials (6 × 11; see Van Gils *et al*. 2003a for more details on this experiment). Foraging behaviour was videotaped (Hi-8; SONY) and tapes were analysed at slow motion (1/5 of recording speed) using 'The Observer' package (Noldus Information Technology 1997). Handling times were recorded to the nearest 0·04 s. For this purpose, we selected the first ingestions only to make handling times in the no-choice-trials comparable to those in the choice-trials (i.e. in this way we prevented effects of satiation on handling time, which may occur after more than 5–10 consecutive ingestions). To obtain least-square mean estimates, handling times were log-transformed and were tested for effects of BIRD-ID.

EXPERIMENT 2: TWO HIDDEN PREY TYPES IN A SINGLE PATCH

The birds and their holding conditions. The four birds that participated in this experiment (7–28 May 1997) were in their second year of life, and were mist-netted at Griend on 9 February 1997, after which they were held in outdoor aviaries at the Royal Netherlands Institute for Sea Research. In early April 1997, approximately 3 weeks before the experiment started, we moved them to a larger outdoor aviary (7 × 7 × 3 m) in which the experiment was carried out. In this aviary we placed 2–3 trays (0·6 × 0·4 m each) and filled those with sediment that we had collected in the nearby Wadden Sea. The basin of the aviary was filled up with seawater to a level just below the top of the trays, such that it would mimic naturally exposed feeding patches. Several times a day we inserted high densities of bivalve prey (mainly *Macoma balthica* and *Cerastoderma edule*) into the sediment, in order to feed the birds and to let them get acquainted with the experimental set-up (which was restricted to one of these trays). During the night (from 9 p.m. to 8 a.m.), the knots were locked in an adjacent 'high-tide roost cage' (4 × 1 × 2 m) that was freely accessible during daytime. This had a sand-covered floor and the birds could drink freshwater here. We weighed the birds daily and adjusted their daily amount of staple food accordingly (as described for experiment 1). Occasionally, when their body masses were low, they were given a handful of trout pellets.

The prey. In the experiment we only used two prey types: small-sized (8 mm) and large-sized (16 mm) *Macoma balthica*. They were collected twice a week on mudflats north-east of Texel. In the laboratory we sorted the appropriate size classes. The rest was used as staple food in between trials. All items were stored in basins filled with aerated seawater (5–12 °C), where they could live for 2–3 weeks. As, on the one hand, the increase in shell mass with length is steeper than the increase in metabolizable energy content mass (flesh mass; Zwarts & Blomert 1992), small-sized *Macoma* are usually of higher digestive quality (e/k) than large-sized *Macoma*. On the other hand, as this increase in

energy content is generally steeper than the increase in handling time (Piersma *et al*. 1995), small-sized *Macoma* are usually of lower profitability (*e*/*h*) than large-sized *Macoma*.

Experimental protocol. Trials were performed with single individuals. Staple food was removed at least 6 h before a trial began. Just before a trial started, we locked the three birds that were not involved into their high-tide roost cage, and put the focal bird in a small cage (1 × 1 × 1 m) placed at one end of the aviary. Once all necessary pretrial preparations were done, we would release the focal bird into its experimental 'arena' by lifting the vertically sliding door of its small cage. It would then fly onto the single experimental tray (0·6 × 0·4 m). This defined the start of a trial.

The tray contained 60 buried *Macoma balthica*, 15 being of the 8-mm class and 45 of the 16-mm class. Such a set-up with the higher quality, but less profitable prey (8 mm) in lowest density conforms to the situation in Fig. 2(D), which enhances the discrimination between predictions of both diet models (i.e. the CM would predict a diet consisting only of the most profitable 16-mm class, while the DRM would predict a diet consisting mostly of the highest quality 8-mm class).

We used the following routine to prepare this experimental tray (cf. Piersma *et al*. 1995). First, prey items were distributed randomly over the patch. Then, by using a little plastic rod with a cm-scale, we inserted the items in their natural position into the sediment to a depth of 1–3 cm. Finally, we sprayed seawater over the sediment surface to mimic a freshly exposed natural mudflat.

From a hide (1 × 1 × 2 m) next to the aviary and 2 m away from the tray we scored which type of prey the focal bird encountered and whether those were accepted or not (this was double-checked by video-analyses, see below). Although trials usually lasted longer, to keep depletion effects small, we stopped each analysis after six prey items had been encountered (i.e. up to 10% of initial density).

Except for one bird that participated in three trials, trials were carried out four times with each bird. This resulted in 15 trials in total (i.e. 15 × 6 = 90 prey choices), of which the order was randomised with respect to individual bird. Proportions of accepted items per prey type were arcsine-square-root transformed before analysis.

Model parameters. In order to predict accepted proportions of encountered prey, we modelled how long-term intake rate (X, Y) is constrained by the combination of digestive capacity c and experimental food environment **F**. Besides each bird's digestive capacity c, we therefore measured the following parameters (per prey type): encounter rate λ (being the product of the controlled prey density D and searching efficiency a), metabolizable energy content e, indigestible ballast mass k, and handling time h.

Digestive capacity. In order to determine digestive processing capacity (c), we ultrasonographically estimated each bird's gizzard size in duplo at 21 May 1997 (as described for experiment 1).

Searching efficiency. In order to calculate searching efficiency we recorded each trial with a Hi-8 video camera (SONY), placed on a tripod in the hide. Videotapes were analysed using 'The Observer' package (Noldus Information Technology 1997). This enabled us to score at slow motion (1/5 of recording speed) and with a precision of 0·04 s how much active search time (i.e. probing, pecking) was required to find each prey item. These search times were averaged over the first six prey encounters per trial. This meant that search times for the two prey types were lumped, which is permissible since searching efficiency in buried bivalves is independent of shell length (Piersma *et al*. 1995). From this average search time (T_s) and initial prey density ($D_i = 60$) we calculated searching efficiency (a) as (Holling 1959):

$$a = \frac{1}{D_i T_s} \qquad \text{(eqn 9)}$$

Note that by using D_i we ignored the effect of prey depletion on T_s (which seems reasonable since only 10% of the prey were taken). These searching efficiencies per trial were $\log_{10}$-transformed and effects of BIRD-ID were subsequently tested in a GLM (cf. Piersma *et al*. 1995).

Energy content & ballast mass. From a subsample of prey items we determined metabolizable energy content (e) and indigestible ballast mass (k) as described for the bivalve species in experiment 1.

Handling time. Estimates for handling time (h) were taken from Piersma *et al*. (1995). The birds used in that study were not the ones used here. However, interindividual differences in handling time are usually very small (see Table 8 in Piersma *et al*. 1995) so using published values on handling time should not affect our conclusions here.

FIELD: MULTIPLE HIDDEN PREY TYPES IN A SINGLE PATCH

Diet composition. Between 9 September and 12 October 1996, dropping samples were collected at five different sites where red knots had recently fed (< 1 h ago). These sites were located close together (at most 280 m apart) at the eastern flat of our main study area, the Grienderwaard, western Dutch Wadden Sea (53°15′-N, 5°19′-E; see also Piersma *et al*. 1993b). Each sample contained 100–200 droppings, and was analysed following Dekinga & Piersma (1993). This allowed us to assign shell fragments to different prey species, and to reconstruct each species' size distribution from unbroken

hinges (to nearest mm). Since food retention times in digestive tracts of knots are short (20–50 min, Piersma 1994) relative to times spent at feeding sites, dropping analysis reliably reveals what knots have been eaten locally.

Model parameters. In order to compare these observed diets with predicted diets, we reconstructed the constraints on short-term intake rate set by food environment **F** from estimates of each prey type's encounter rate λ (being the product of prey density D and searching efficiency a), metabolizable energy content e, indigestible ballast mass k, and handling time h. The additional digestive constraint c on long-term intake rate was estimated from gizzard sizes of red knots collected in the Wadden Sea in Sep–Oct (Van Gils *et al*. 2003a).

Prey density. At each site we estimated available prey density (D) during the same low tide period in which the droppings for that site were collected. Given that large flocks of foraging knots can reduce prey densities by 25% during a single low tide (Van Gils *et al*. 2003b), we estimated at each site initial and final prey density (i.e. giving-up density) to obtain an accurate estimate of average prey density during exploitation. Initial prey density was estimated in a reference area of 100 m^2, from which knots were excluded by a peg and rope 'fence' at knot-height. Final prey density was estimated just next to the exclosure (within 10 m; for more details see Van Gils *et al*. 2003b). At each site we took 50 subsamples inside, and 50 subsamples outside the exclosure (such subsample sizes guarantee standard errors that are 5–10% of the mean; Piersma *et al*. 1993b). Each subsample contained sediment taken to a depth of 20 cm with a core of 1/56 m^2. This sediment was sliced into a top layer (0–4 cm; containing the accessible prey) and a bottom layer (4–20 cm) which were sieved separately over 1-mm mesh. In the laboratory, we sorted all prey items to species-size categories, i.e. prey types (to nearest mm, using callipers). We only considered the two most abundant prey species (*Cerastoderma edule* and *Mya arenaria*) that together had 26 prey types available which represented the majority of the total, locally available biomass (i.e. accessible and ingestible; Zwarts & Wanink 1993). Largest ingestible prey types were taken as the 16-mm type for *Cerastoderma* and the 20-mm type for *Mya* (Zwarts & Blomert 1992).

Searching efficiency. We used the estimate for searching efficiency (a) that we obtained in experiment 2.

Energy content & ballast mass. From prey items collected throughout Grienderwaard in Jul–Nov 1996 as part of a larger survey (Piersma *et al*. 2001), we determined metabolizable energy content (e) and ballast mass (k) as described for the bivalve species in experiment 1.

Handling time. Size-specific handling times (h) on *Cerastoderma* were taken from Piersma *et al*. (1995). Size-specific handling times on *Mya* are assumed to be similar to those on similarly shaped *Macoma balthica* (Piersma *et al*. 1995). For both prey species we took into account that handling buried bivalves requires at least 2 s (Zwarts & Blomert 1992).

Digestive capacity. In order to estimate the population's average digestive processing capacity (c), we estimated gizzard size of red knots living in the Wadden Sea by either carcass analysis ($N = 12$; collected in 1990–92), or by ultrasonography ($N = 75$; collected in 2001–02; see exp. 1 for methodology). Since gizzard masses show strong seasonal variation (Van Gils *et al*. 2003a), we restricted our sample only to those birds that were caught in September or October.

Results

EXPERIMENT 1: *AD LIBITUM* EXPOSED PREY IN A SINGLE PATCH

Digestive capacity. Across the six birds, average gizzard mass was 4·30 g (SE = 0·88 g; range = 2·7–6·1 g), which translates into a digestive processing capacity (c) of 0·94 mg ballast/s (Van Gils *et al*. 2003a). Over time, there was no significant change in digestive capacity (average change in gizzard mass ±SE = 0·6 ± 0·9; $P > 0{\cdot}55$; $N = 6$).

Energy content & ballast mass. Estimates of metabolizable energy content (e) and indigestible ballast mass (k) are presented in Fig. 3(A)–(J).

Handling time. Although handling time (h) varied between individual birds for 6 out of the 11 prey types ($P < 0{\cdot}05$), these differences were due to only 17 of the $165\left(11 \times \binom{6}{2}\right)$ Bonferroni pairwise comparisons (10%). This allowed us to proceed with the general estimate of handling time per prey type (Fig. 3K–O).

Choice predicted. From these prey characteristics (e, k, and h) we derived energy and ballast intake rates while handling (e/h and k/h; Fig. 3P–Y). These represent the only constraints on, respectively, energy and ballast intake rate while foraging (since no search time was required). Comparing these with the constraint on long-term ballast intake rate set by gizzard size (Fig. 4) shows that $k_i/h_i > c$ for all prey types (i.e. the gizzard is unable to keep up with the rate of handling). This conforms to the situation in Fig. 2(B), in which the DRM predicts prey preference to be a function of digestive quality (e/k), while the CM predicts it to be a function of profitability (e/h; cf. Fig. 2A).

Choice analysed. In contrast to predictions of the CM and in agreement with those of the DRM, prey preference was not related to profitability (Table 1A, Fig. 5A), but to quality (Table 1B, Fig. 5B). In both tests there was no effect of individual bird.

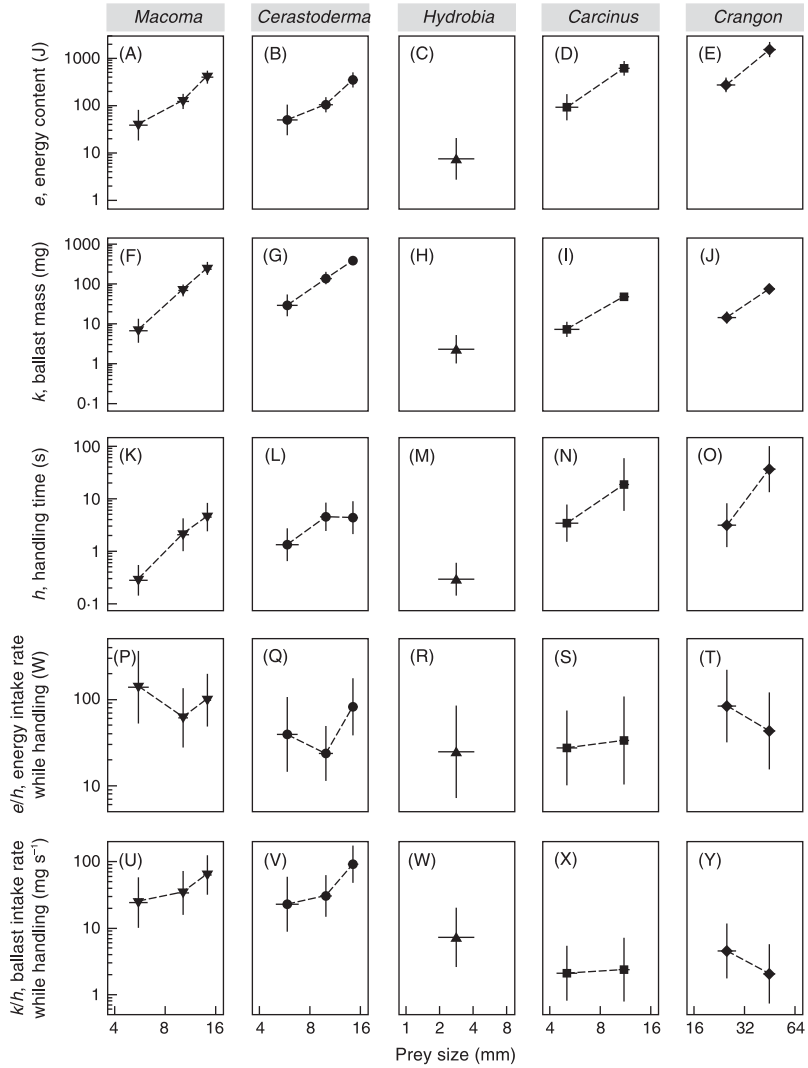

Fig. 3. Five prey characteristics (± SD) in relation to their size (mm; ± SD) for each of the five prey species (11 types) that were used in experiment 1. Note that energy (A–E and P–T) refers to metabolizable energy. Energy intake rate while handling (P–T) is equivalent to profitability.

EXPERIMENT 2: TWO HIDDEN PREY TYPES IN A SINGLE PATCH

Digestive capacity. Across the four birds, average gizzard mass was 6·65 g (SE = 0·47), which translates into a digestive processing capacity (c) of 2·28 mg ballast/s (Van Gils *et al*. 2003a).

Energy content & ballast mass. Average 8-mm *Macoma* contained 4·9 mg of flesh mass (SE = 0·7, $N = 6$) and 16·9 mg of indigestible ballast mass (SE = 1·9, $N = 4$). Average 16-mm *Macoma* contained 52·5 mg of flesh mass (SE = 3·3, $N = 11$) and 265·5 mg of indigestible ballast mass (SE = 17·9, $N = 10$). Thus, as planned, the higher quality type (i.e. 8-mm class; $e/k = 4{\cdot}6$ J mg^{-1}) was not as profitable ($e/h = 57{\cdot}0$ W) as the lower-quality type (i.e. 16-mm class; $e/k = 3{\cdot}2$ J mg^{-1}; $e/h = 152{\cdot}7$ W).

Searching efficiency. Searching efficiency (a) did not vary among birds (Table 2). We therefore excluded BIRD-ID from the general linear model to obtain the $\log_{10}$-transformed least square mean estimate. Applying bias correcting back-transformation (i.e. antilog(estimate + 2·303 × variance/2)) led to a searching efficiency of 10·46 cm^2 s^{-1}.

Table 1. Analyses of variance in cardinal preference ranks α_i in experiment 1. (A) Profitability (W) is $\log_{10}$-transformed and treated as a continuous variable. BIRD-ID is treated as a categorical variable. (B) Digestive quality (J mg^{-1}) is $\log_{10}$-transformed and treated as a continuous variable. BIRD-ID is treated as a categorical variable

Independent variable	SS	d.f.	*P*
(A) Profitability	52·53	1	0·578
BIRD-ID	749·43	5	0·491
Error	9881·72	59	
(B) Quality	3373·07	1	< 0·001
BIRD-ID	749·43	5	0·257
Error	6561·17	59	

SS, sum of squares; d.f., degrees of freedom; *P*, significance probability.

Table 2. Analysis of variance in ($\log_{10}$-transformed) searching efficiency in experiment 2. BIRD-ID is treated as a categorical variable. SS is sum of squares, d.f. is degrees of freedom, and *P* is significance probability

Independent variable	SS	d.f.	*P*
BIRD-ID	0·734	3	0·053
Error	0·765	11	

Choice predicted. We estimated constraints on intake rate (*X*, *Y*) while actively foraging from estimates of each prey type's e_i, k_i, h_i and λ_i. Comparing this feasible set of short-term intake rates with upper ballast-processing rate *c* (Fig. 6) shows that knots would maximize their long-term energy intake rate *Y* by accepting each item of the high-quality prey ($p_{8\text{-mm}} = 1$) while ignoring virtually all items of the low-quality prey ($p_{16\text{-mm}} = 0{\cdot}057$; a situation comparable to Fig. 2D). These predictions of the DRM contrast those of the CM wherein only the low-quality, but highly profitable, type should be accepted ($p_{16\text{-mm}} = 1$; comparable to Fig. 2C).

Choice analysed. Proportion p_i of prey items accepted was 0·989 for the 8-mm type (arcsine transformed mean ±SE: 1·465 ± 0·090), while only 0·009 for the 16-mm type (arcsine transformed mean ±SE: 0·094 ± 0·083). This is in agreement with predictions of DRM (respectively $P > 0{\cdot}2$ and $P > 0{\cdot}05$) but conflicts with those of the CM ($P < 0{\cdot}0001$ for both types; Fig. 7).

FIELD: MULTIPLE HIDDEN PREY TYPES IN A SINGLE PATCH

Digestive capacity. Average gizzard mass of knots living in the Wadden Sea in Sep–Oct was 7·26 g (SE = 0·21, *N* = 87), which translates into a digestive processing capacity (*c*) of 2·68 mg ballast/s (Van Gils *et al.* 2003a).

Energy content & ballast mass. Allometric relations for flesh and ballast mass are presented in Table 3.

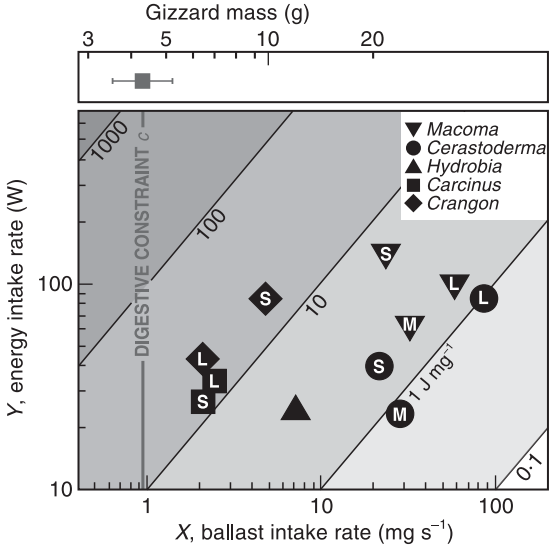

Fig. 4. From mean gizzard mass (grey square ± SE) we derived the birds' digestive processing capacity *c* (vertical line) in experiment 1. Ballast intake rate while handling (k/h) each of the 11 prey types exceeds this constraint-level. Experimental conditions are thus similar to those in Fig. 2(B): prey preference should be a function of prey quality only (and not of profitability). Note that we used a log-log scale for reasons of presentational clarity. A linear scale is recommended when predicting which prey type should be preferred most (cf. Figs 1, 2), since then digestive prey quality is simply reflected by the angle to origin of the graph (on this log-log scale it is reflected by solid lines with unity slope). Letters in symbols refer to prey size: S = small, M = medium-sized, and L = large.

Choice predicted. From constraints set by food environment **F** ($[e_i, k_i, h_i, \lambda_i]$) we reconstructed the range of feasible intake rates (*X*, *Y*) while foraging (loop in Fig. 8). Adding the long-term digestive processing constraint (*c*; vertical line in Fig. 8), showed that $c < X^*$, i.e. that gizzard sizes were not sufficient to keep up with rate of ballast intake that maximized rate of energy intake while foraging (Y^*). If gizzard sizes were never limiting, the CM-diet, which would have included all but the least profitable prey types (i.e. those 5-mm), would

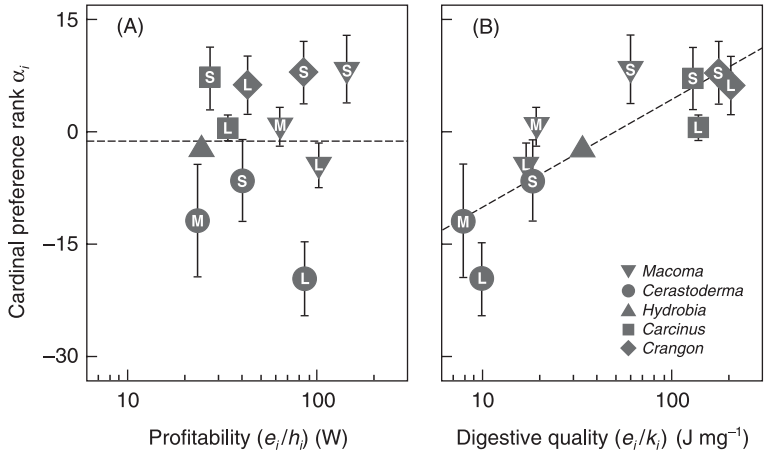

Fig. 5. (A) Cardinal preference ranks α (± SE) are not related to profitability (W). (B) but to digestive quality (J mg^{-1}). Dashed lines are linear regressions (Table 1A–B).

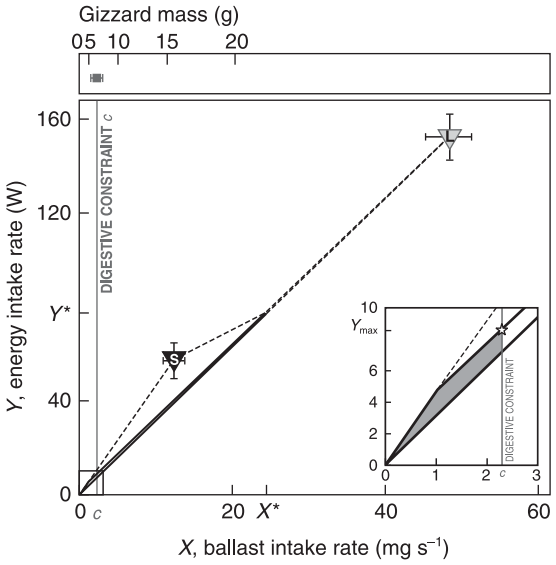

Fig. 6. From mean gizzard mass (grey square ± SD) we derived the birds' digestive processing capacity c (vertical line) in experiment 2. This capacity constrains rate of energy intake in the same way as in Fig. 2(D): experimental birds would maximize long-term energy intake if they followed the DRM and completely accepted small prey type S (8-mm size class, solid triangle, $p_S = 1$) and only partially preferred large type L (16-mm size class, grey triangle, $p_L = 0{\cdot}057$). Note that this is almost entirely opposite to predictions of the CM, which would predict $p_S = 0$ and $p_L = 1$ for such experimental conditions (critical profitability threshold = Y^*). Dashed lines are drawn to guide the eye, and bars denote SE. In inset, grey area indicates range in sustainable long-term intake rates, and star indicates maximum long-term energy intake rate that is obtained when the DRM is followed.

have been optimal. Instead, a DRM-diet, in which largest (> 12 mm) and smallest (4 mm) low-quality *Cerastoderma* are ignored, is optimal in this case (Fig. 8).

Choice analysed. The observed diet comprised mostly high-quality *Mya* and only small amounts of low-quality *Cerastoderma* (only medium size classes; Fig. 9D). This is in agreement with predictions of the DRM (Fig. 9C; $P > 0{\cdot}6$ one-sample t-test with $N = 5$) and not with those of the CM (Fig. 9B; $P < 0{\cdot}001$ one-sample t-test with $N = 5$).

Discussion

RED KNOTS OBEYED THE RULES OF THE DRM

Each of three tests supported the DRM and refuted the CM. Short-term ballast intake rates in the first experiment were too high for the digestive system to be able to keep up (especially since no search times were required; Fig. 4). In such a context, the DRM predicts long-term rate-maximizing foragers to prefer those prey types that yield high energy-assimilation rates, in other words prey types that contain high amounts of flesh relative to their ballast mass (digestive quality *e*/*k*; Fig. 2B), such as *Crangon* and *Carcinus* (Figs 3–5). On the contrary, while ignoring the role of a digestive constraint, the CM predicts such foragers to prefer prey types that are highly profitable, i.e. types that contain high amounts of energy relative to required handling time (*e*/*h*; Fig. 2A), such as large *Macoma* and large *Cerastoderma* (Figs 3–5). In line with the DRM, preference of the experimental birds reflected digestive quality and not profitability (Fig. 5).

Since some search time was required in the second experiment, short-term intake rates were not as high as in the first experiment. Therefore, feeding only on highest quality prey (small *Macoma*) was not constrained by rate of digestion, and therefore the inclusion of a fraction of lower quality, but more profitable prey (large *Macoma*) maximized long-term energy intake (DRM; Fig. 6 cf. Fig. 2D). The CM predicted a complete absence of highest quality prey from the diet (cf. Fig. 2C). In line with the DRM, the experimental birds ate virtually all encountered small *Macoma* while ignoring most large *Macoma* (Fig. 7). As a methodological aside, we note that searching efficiencies that we measured here ($a = 10{\cdot}5$ cm^2 s^{-1}) were double those observed by Piersma *et al.* (1995; $a = 5{\cdot}2$ cm^2 s^{-1}). This

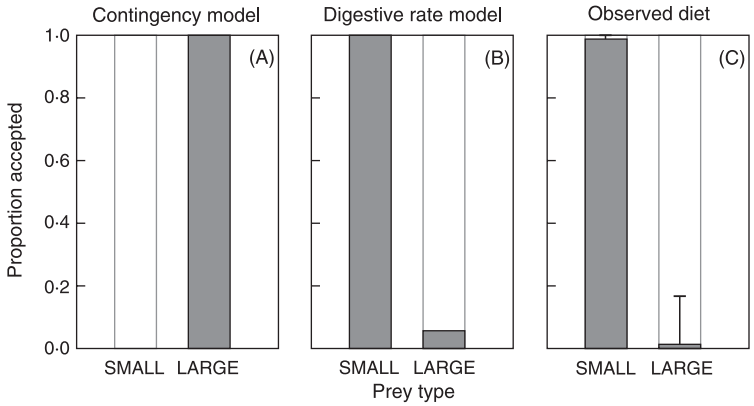

Fig. 7. (A). Predictions of the CM for experiment 2: small prey type (8-mm size class) should be completely rejected ($p_S = 0$) and large type (16-mm size class) should be completely accepted ($p_L = 1$). (B). Predictions of the DRM are almost entirely opposite: $p_S = 1$ and $p_L = 0{\cdot}057$. (C). Observed prey preferences (backtransformed averages ± SD) do not match predictions of the CM but those of the DRM.

Table 3. Observed $\log_{10}$–$\log_{10}$ relationships for flesh and ballast mass (mg) as a function of shell length (mm) of *Cerastoderma* and *Mya* collected in Jul–November 1996 at Grienderwaard

Species	Part	Constant	Slope	N	R^2	F-ratio	P
Cerastoderma	$AFDM_{flesh}$	−1·781	2·724	59	0·795	221·516	< 0·001
Cerastoderma	k	−1·383	3·535	57	0·858	333·249	< 0·001
Mya	$AFDM_{flesh}$	−1·861	2·617	97	0·663	186·936	< 0·001
Mya	k	−1·067	2·512	36	0·674	70·305	< 0·001

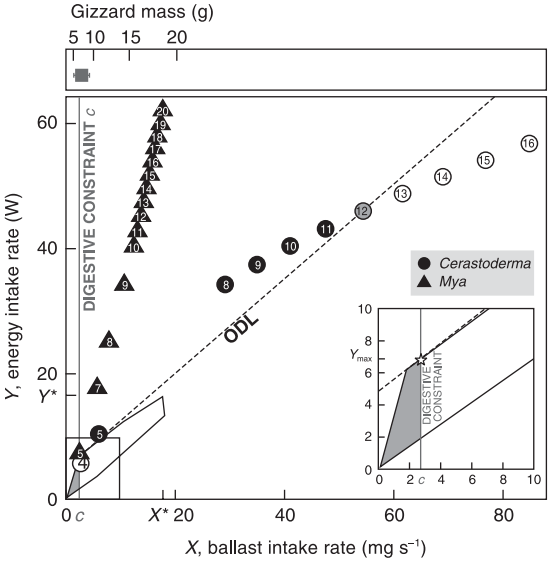

Fig. 8. From mean gizzard mass in the field (grey square ± SD; Sep–Oct) we derived the birds' digestive processing capacity c (vertical line). As this capacity (2·7 mg s^{-1}) is insufficient to keep up with rate of ballast intake (17·4 mg s^{-1}) at an energy-maximizing diet (Y^* = 16·6 W), optimal foraging knots should follow the DRM and use the diagonal ODL as their critical threshold to obtain highest sustainable long-term intake rate (Y_{max} = 6·8 W; star in inset). This means that all available *Mya* (triangles) should be accepted (p_i = 1; numbers in symbols indicate shell length in mm), and that only medium-sized *Cerastoderma* (dots) should be completely (5–11 mm; p_i = 1; filled dots) or partially (12 mm; $p_{12\text{-mm}}$ = 0·49 grey dot) accepted. This is in sharp contrast to the predictions of the CM, according to which prey types whose profitability exceeds Y^* should be included, which concerns virtually all types. Note that for reasons of presentational clarity we have plotted only one feasible loop (i.e. one prey density sample) instead of all five. Densities of different prey types did not differ between samples so loops are almost identical.

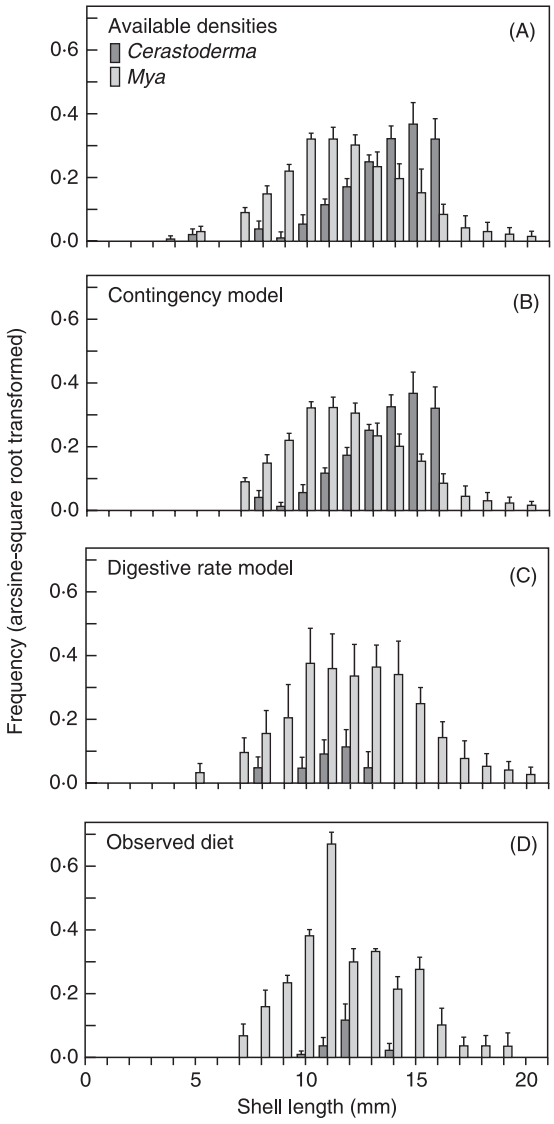

Fig. 9. Observed size distributions per prey species (arcsine square root transformed; ± SE) in (A) available prey densities (B) diet predicted by the CM (C) diet predicted by the DRM, and (D) observed diet.

is presumably due to a more accurate video-analysing technique applied in the present study, that allowed us to score short interruptions in searching (0·1–0·2 s) that would otherwise be unnoticed.

Since red knots in the two-prey-species context in the wild faced a digestive bottleneck they should follow the rules of the DRM in order to maximize long-term energy intake rate. This implies that they should ignore the majority of low quality *Cerastoderma* (smallest and largest available size classes) while accepting all of the available high quality *Mya* (Figs 8, 9). The CM predicts that only the smallest size classes of *Cerastoderma* and *Mya* should be ignored (Figs 8, 9). In line with the DRM, the diet of those free-living knots was mainly composed of *Mya* (Fig. 9).

IS THE DRM APPLICABLE TO OTHER ANIMALS?

Only a few and recent tests of the DRM have been applied and those have all been restricted to mammalian

herbivores (Fortin *et al*. 2002; Illius *et al*. 2002). On the contrary, many tests of the CM have been performed in a wide range of foragers (see reviews by Stephens & Krebs 1986; Maurer 1996; Sih & Christensen 2001). Only about half of those CM-tests corroborated the model's predictions (Maurer 1996; Sih & Christensen 2001). One reason for this high falsification rate might be that the CM is only valid in case of handling-limited foraging. Accepting Jeschke *et al*.'s (2002) conclusion that animals are mostly digestion- rather than handling-limited, suggests that the DRM will be a helpful model in a wide range of species, especially those that swallow large amounts of refractory (ballast) material, such as herbivores, but also granivores, insectivores and some carnivores (Karasov & McWilliams 2004). Especially studies on mollusc-eating shorebirds (Navarro, Velasques & Schlatter 1989; Dierschke 1993; Leinaas & Ambrose 1999) or on other avian molluscivores (Pierotti & Annett 1991; Beauchamp, Guillemette & Ydenberg 1992) may want to reinterpret their results in the light of the DRM. Moreover, conclusions from theoretical predator-prey studies that assume a CM-scenario (Genkai-Gato & Yamamura 2000; Křivan & Eisner 2003) might alter drastically when taking digestive constraints into account.

For example, preference for the least profitable, small freshwater mussels by shellfish-eating ducks (*Aythya* spec.) could not be explained by the CM (Draulans 1982, 1984; De Leeuw 1999). As these ducks ingest their prey whole, just as knots, their energy intake rates are likely to be constrained by rates at which bulky shell material can be processed. Given that shell mass increases more steeply with prey size than does flesh mass (De Leeuw 1999), those smallest mussels are of highest digestive quality. This seems a likely explanation for what Draulans (1984) has called 'suboptimal' size selection.

An interesting exception to which the CM has been successfully applied is the molluscivore oystercatcher (*Haematopus ostralegus*, e.g. Cayford & Goss-Custard 1990; Wanink & Zwarts 2001). The reason for this success is straightforward: this shorebird species only consumes the bivalve's flesh by removing it from the shell (Norton-Griffiths 1967). This leads to CM being valid as (1) rates of digestion are not bottlenecked by processing bulky shell material, and (2) relatively long external handling times are required (Zwarts *et al*. 1996a). Therefore, most profitable (e/h) and thus most preferred prey are items whose shell can be removed quickly (Wanink & Zwarts 1985), or, even better, items that have no shell at all (e.g. leatherjackets and worms; Zwarts *et al*. 1996a). It is interesting to contrast this to red knots that also prefer soft-bodied prey types most (*Carcinus* and *Crangon*), but then for reasons of digestive quality (e/k; experiment 1).

Another point to make is that even though shell material cannot cause digestive constraints in oystercatchers, there is good evidence that rates of flesh assimilation do constrain their daily energy intake (Kersten & Visser 1996; Zwarts *et al*. 1996b). The fact that under such circumstances predictions of the CM are still confirmed may at first seem puzzling. However, in contrast to knots, oystercatchers possess a large proventriculus (glandular stomach), where they store considerable amounts of flesh (about half of the food collected in a single low tide period; Zwarts *et al*. 1996b), which enables them to partly postpone digestion to the period of rest during high tide. Therefore, maximizing total amount of energy assimilated over a full tidal cycle may require a filled-up proventriculus at the end of the low tide period. Likely, this may be accomplished most effectively by rapid prey collection (i.e. following the CM) and not by selecting easy-to-digest prey (i.e. following the DRM).

Acknowledgements

We are grateful to Nanda Scheerder and Petra Eckenhaussen for their support during experiments, and to Oscar Bos and many volunteers for their assistance in the field. Bernard Spaans and Peter van der Puyl are acknowledged for technical assistance. We thank Dick Visser for drawing the figures and two anonymous referees for comments on the manuscript. This study was supported by a PIONIER-grant from the Netherlands Organization for Scientific Research (NWO) to TP. Experiments fulfilled legal Dutch requirements.

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Received 27 November 2003; accepted 28 June 2004